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Decreased wheat grain yield stimulation by free air CO_2 enrichment under N deficiency is strongly related to decreased radiation use efficiency enhancement

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ABSTRACT

Uncertainty still exists about the extent and mechanisms of yield stimulation by elevated atmospheric CO_2 (e[CO_2]) in wheat. Particularly, data of the e[CO_2] effect under severe N deficiency from field experiments are scarce. To investigate the interaction of e[CO_2] and N fertilization on important variables that determine grain yield and are often used in crop simulation models, e.g. radiation absorption by the canopy (AR), radiation use efficiency (RUE) and specific leaf N weight (SLNW), a two-year Free Air CO_2 Enrichment (FACE) experiment was conducted with two [CO_2] (393 and 600 ppm) and three N levels (severe N deficiency (Nd) with 40 (1st year) and 35 kg N ha^{-1} (2nd year); adequate N supply with 180 (1st year) and 200 kg N ha^{-1} (2nd year); and excess N supply with 320 kg N ha^{-1} (1st and 2nd year).

Final aboveground biomass ranged from 816 to 2012 g m^{-2} and grain yield from 417 to 973 g m^{-2}. e[CO_2] increased aboveground biomass by 13, 18 and 14% and grain yield by 10, 17 and 17% under Nd, Nad and Nex, respectively. Yield stimulation was primarily due to enhanced grain number. With increasing N supply, peak values of green area index were increased under e[CO_2] by 4 up to 22%, while AR was unaffected. RUE was increased by both rising SLNW, which depended on N supply, and e[CO_2] and the RUE increase was larger under Nad (+20%) and Nex (+18%) than under Nd (+6%). SLNW was decreased by e[CO_2] and this decrease was very similar among N levels (~ −6%). However, if leaf area index was included as covariable, then a e[CO_2] induced decrease of SLNW was only found under Nd.

The present study demonstrates that yield stimulation by e[CO_2] is smaller under severe N deficiency compared to high N supply in wheat. In contrast to the results of another FACE study, this decrease was not due to reduced AR but reduced RUE, which might be attributed to both restrictions on source activity, i.e. photosynthetic capacity and sink size, i.e. ear growth.

1. Introduction

Atmospheric CO_2 concentration is continuing to rise from current 400 up to 730–1020 ppm by the end of this century (IPCC, 2013). Elevated CO_2 concentration (e[CO_2]) will increase air temperature and thus possibly the frequency and severity of weather extremes that could reduce future crop yields (IPCC, 2013). On the other hand, e[CO_2] increases photosynthesis in C_3 plants (Ainsworth and Long, 2005) and reduces stomatal conductance in C_3 and C_4 plants (Ainsworth and Rogers, 2007; Wang et al., 2013), which often lead to stimulation of biomass production and grain yield (Ainsworth and Long, 2005; Manderscheid et al., 2014).

Wheat is the third most important crop in terms of global production and its range of cultivation plays a key role for food security (Shewry and Hey, 2015). Crop models predict that growth stimulation of C_3 crops by e[CO_2] will compensate for yield losses due to rising air temperature up to 2 °C, but the extent of this compensation might be different depending on the region and its related agricultural conditions such as N fertilizer availability (Rosenzweig et al., 2014). Therefore, uncertainty still exists about the extent of wheat yield stimulation by future e[CO_2]. Free Air CO_2 Enrichment (FACE) experiments can help to overcome this uncertainty and were conducted with wheat in

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Arizona (Kimball et al., 2002), Australia (Tausz-Posch et al., 2012), China (Kou et al., 2007; Ma et al., 2007; Lam et al., 2012; Han et al., 2015; Cai et al., 2016) and Germany (Högy et al., 2009; Weigel and Manderscheid, 2012). However, comprehensive growth data from such studies, especially those on the interactions between e[CO_2] and N fertilization, are still scarce (Rosenzweig et al., 2014; Vanuytrecht and Thorburn, 2017).

Grain yield (Y) can be described as a function of three factors describing fundamental processes: (i) absorbed photosynthetic active radiation (PAR) accumulated over the growing season (AR), (ii) conversion efficiency of AR to biomass (radiation use efficiency: RUE) and (iii) share of produced biomass allocated to the grains (harvest index: HI):

$$Y = AR * RUE * HI \quad (1)$$

AR is determined by the size and evolution of the green area index (GAI), the sum of the green surfaces of leaves, stems and ears. RUE increases with rising light-saturated net photosynthetic rate in a curvelinear manner (Sinclair and Horie, 1989) and both variables depend on both the leaf biochemical composition such as level and activity of ribulose-1,5-bisphosphate carboxylase/oxygenase (RuBisCO) and the internal structure of the leaf. Easily determinable proxies for the variables describing the leaf biochemical composition and internal structure are green leaf N concentration, leaf mass per unit leaf area (specific leaf weight) and their composite variable leaf N mass per unit leaf area (specific leaf N weight). Increase in soil N availability stimulates crop growth primarily by increasing the size and duration of GAI and thus AR (Garcia et al., 1988; Jamieson et al., 2000). RUE is not influenced over a broad range of leaf and soil N levels, but declines sharply when these N levels become very low (Sinclair and Horie, 1989). Effects of e[CO_2] are expressed primarily through effects on RUE via influencing the activity of RuBisCO (Long, 1991; Jamieson et al., 2000).

Variation in grain yield due to e[CO_2] is primarily due to variation in grain number (Högy et al., 2009; Cai et al., 2016), but some studies also found e[CO_2] effects on individual grain weight (Fernando et al., 2014; Tausz-Posch et al., 2015). Grain number is strongly associated with growth between flag leaf emergence and anthesis (Bindraban et al., 1998), the period in which radiation supply (Fischer, 1975) and e[CO_2] (Fischer and Aguilarm, 1976) have their greatest influence on grain number.

CO_2 enrichment studies with chambers (Sionit et al., 1981; Wolf, 1996) and FACE (Kimball et al., 2002; Weigel and Manderscheid, 2012) showed that growth stimulation of wheat by e[CO_2] declined when N supply decreased. Kimball et al. (2002) reported for the Arizona FACE study, the only previous FACE study that had a severe N deficiency treatment, that the grain yield increase under e[CO_2] was only half as much under severe N deficiency compared to ample N supply. Nevertheless, FACE studies showed similar biomass and grain yield increases under e[CO_2] in plants grown under low and high N supply (Ma et al., 2007; Han et al., 2015). In the two-year FACE study of Weigel and Manderscheid (2012) lower grain yield stimulation under moderate N deficiency as compared to adequate N supply was only observed in one year.

While AR, RUE and harvest index are important parameters used in many crop models, only little experimental data from FACE experiments related to these parameters exists (Vanuytrecht et al., 2012), which might be responsible for the poor representation of CO_2 x N interactions in crop growth models (Rosenzweig et al., 2014; Vanuytrecht and Thorburn, 2017). According to Jamieson et al. (2000), the smaller grain yield stimulation of e[CO_2] under severe N deficiency in the Arizona FACE experiment was due to reduced AR because of accelerated canopy senescence under e[CO_2]. Moreover, in the same experiment e[CO_2] reduced leaf N concentration by up to -25% (Kimball et al., 2002) under severe N deficiency when leaf N levels were low (Sinclair et al., 2000), but there was hardly any reduction of leaf N concentration by e[CO_2] under ample N supply (Kimball et al., 2002). Based on these findings, it was concluded that photosynthetic capacity is primarily reduced by e[CO_2] under very low N availability (Rubio-Asensio and Bloom, 2016), which might result in smaller stimulation of RUE by e[CO_2] under such N levels compared to high N supply. However, there is no field study available for wheat that has investigated in wheat the CO_2 x N interaction on RUE. Because limited N fertilizer levels are affordable in many developing countries, investigating e[CO_2] effects on yield formation under severe N deficiency is of overall importantance to provide more accurate predictions of future global food security.

In the present study a two-year FACE experiment was conducted with winter wheat (*Triticum aestivum* L.) under irrigated agriculture to avoid interactive effects with water stress supplied with three levels (severe deficiency, adequate, excess) of N fertilizer. The main objective was to analyze how e[CO_2] influences growth and yield formation under a broad range of N fertilizer levels, and in particular whether and to what extent growth and yield stimulation by e[CO_2] is lower under severe N deficiency compared to high N supply. Moreover, the specific question was addressed: is lower grain yield stimulation by e[CO_2] under severe N deficiency associated with (i) decreased AR under e[CO_2] due to accelerated canopy senescence or (ii) reduced RUE stimulation by e[CO_2] compared to high N supply due to a strong decrease of leaf N concentration?

2. Material and methods

2.1. Study site and experimental design

The experiment was conducted on a field site (52°18′N, 10°26′E, 79 m.a.s.l.) at the Thünen-Institute in Braunschweig, Germany in 2014 and 2015. The soil profile has a depth of about 60 cm (30 cm Ap, 15 cm Al, 15 cm Bt, and > 60–70 cm CII) and the lower layers are almost pure sand. The soil in the plough horizon (0–40 cm) is a luvisol of loamy sand texture (69% sand, 24% silt and 7% clay) with a pH of 6.88, and a carbon and nitrogen (N) content of 1.00% and 0.09%, respectively. Soil N levels at the beginning of the main growing season (mid-March) were 14.2 and 22.4 kg N ha^{-1}. The lower (−1.5 MPa soil water tension) and upper limit (0.01 MPa soil water tension) of plant available soil water are a volumetric soil water content of 5 and 23%, respectively. The soil water amount in the 0–40 cm soil profile at the beginning of the main growing season was 92 mm. Altogether, the soil has low to intermediate fertility with a shallow rooting zone.

Winter wheat (*Triticum aestivum* L. variety “Batis”) was grown at ambient [CO_2] and e[CO_2] in circular plots (diameter 20 m), in which three N subplots (3 m × 5 m) were randomly established. Overall the experiment consisted of six different CO_2 x N treatments that were replicated three times. The CO_2 and N treatments had the same position on the field site in 2014 and 2015.

2.2. CO_2 enrichment

CO_2 enrichment was carried out with a Free Air CO_2 Enrichment (FACE) system with blowers constructed according to the Brookhaven National Laboratory design (Lewin et al., 1992). CO_2 enrichment started from the four leaf stage on March 31 in 2014 and the three leaf stage on March 12 in 2015. CO_2 enrichment took place during the day and was interrupted when wind speed exceeded 6 m s^{-1} or air temperature fell below 5 °C. The 1 min average [CO_2] in the e[CO_2] plots was within 600 ppm ± 10% for 95.6% of the operation time in 2014 and 95.7% for the one in 2015. During the CO_2 enrichment period, average [CO_2] in the ambient plots was 394 in 2014 and 392 ppm in 2015.

2.3. Crop management

Winter wheat was sown with a density of 380 kernels per m^{-2} on October 29 in 2014 and on November 4 in 2015. Crop management measures were performed according to local farm practice with

Table 1
Important cultivation measures and growth stages.

Event		Date	
Management	Phenological phase	2014	2015
Sowing		Oct 29	Nov 4
	Emergence	Nov 18	Nov 19
Start CO_2 enrichment	4 leaf/3 leaf stage	Mar 31	Mar 12
	1st node stage	Apr 18	Apr 30
1st fungicide treatment		Apr 29	Apr 31
	Flag leaf stage	May 14	May 21
2nd fungicide treatment		–	June 4
	Anthesis	June 6	June 12
	Milk ripe stage	June 23	June 30
End of CO_2 enrichment		July 21	July 24
	Grain maturity	July 21	July 27

pesticide applications and adequate nutrient supply based on analysis of soil nutrient content (Ca, K, Mg, P, S) determined in early springtime. Table 1 presents important cultivation measures and plant developmental stages of the experiment. In both years, N fertilization was implemented by manual application of calcium ammonium nitrate (CAN, 27% N). The experiment had three N fertilizer levels: severe deficiency (Nd) with 40 kg N ha^{-1} in 2014 and 35 kg N ha^{-1} in 2015, adequate (Nad) with 180 kg N ha^{-1} in 2014 and 200 kg N ha^{-1} in 2015, and excess N supply (Nex) with 320 kg N ha^{-1} per year. The adequate N fertilizer level corresponds to the amount commonly applied in German agriculture. Because of low grain protein concentration in 2014, the last N dose was increased by 20 kg N ha^{-1} in 2015 under Nad. To prevent drought stress plant available volumetric soil water content was kept in the range of 50 up to 90% of field capacity by manual irrigation. Irrigation and precipitation as well as monthly mean temperature and irradiance over the main growth season are presented in Table 2. These data measured at 2 m height near to the field site of the experiment (< 500 m) were provided by the German Weather Service. Volumetric soil water content in the 40 cm soil profile was measured twice a week with time domain reflectometry (TDR) sensors. Irrigation requirements were forecast by means of the AMBAV model (Kersebaum et al., 2005) by the German Weather Service.

Heavy rainfall caused lodging of the plants grown under excess N supply on July 5 in 2015. To minimize lodging effects on grain growth, these plants were erected by means of a rope net until final harvest.

2.4. Analysis of crop growth

Samplings were conducted at 1st node stage, flag leaf stage, anthesis, milk-ripe stage and final harvest at grain maturity. The sampling area was 1.8 m^2 at final harvest and 0.5 m^2 at the four samplings. At each sampling a subsample (25% of the harvest) was separated into stem (including leaf sheath), leaf lamina and ear (if present). The green surface area of these subsample fractions was determined with a leaf area meter (Model LI-3100, LICOR, USA) followed by biomass determination after drying at 105 °C. The remaining sample was dried at 105 °C followed by biomass determination. Green area index of leaf (LAI), stem (SAI) and ear (EAI) and its sum green area index (GAI) were calculated on the basis of the green surface area and biomass of the plant fractions of the subsample and biomass of the main fraction. Stand height was measured at anthesis by putting a polystyrene disc on top of the plant stand and measuring the distance between polystyrene disc and soil surface. In each subplot, stand height was measured at three random positions.

At grain maturity ears from the 1.8 m^2 sampling area were counted, weighed and stored at room temperature before threshing and determination of yield components. After threshing, the grain and chaff fraction were determined by weight and dry weight determined from a 100 g grain and 200 g chaff subsample after drying at 105 °C. Grain number of the 100 g subsample was determined with a seed counter (model CONTADOR, PFEUFFER, Germany). 1000 grain weight (TGW) was calculated by means of the grain number and the subsample biomass. Grain number per m^2 ground area was calculated on the basis of TGW and grain yield.

Plants were regularly examined for fungal infestations. At the milk-ripe stage in 2015, infestations with *Gaeumannomyces graminis* were detected. To overcome this problem, infested plants were sorted out followed by counting the infested and healthy plant fractions. The maximum share of infested plants of a subplot was less than 15%. Yield variables were determined on the basis of the fraction of healthy plants and were then normalized to total plant number (healthy + infested plants).

2.5. Determination of photosynthetic active radiation absorption, radiation use efficiency and harvest index

The fraction of photosynthetic active radiation (PAR) absorbed by the green canopy (f_{ar}) was measured with a line quantum sensor (model SUNSCAN, DELTA-T-DEVICES, USA). Measurements were conducted every week on sunny days from 1st node stage up to grain maturity. Each measurement included the PAR irradiance above the green canopy (I_o), the PAR irradiance below the green canopy (I_c) and the PAR irradiance reflected by the canopy (I_r) and this was repeated three times per plot. Based on the measured parameters, f_{ar} was calculated by the following equation:

$$f_{ar} = \frac{(I_o - I_c - I_r)}{I_o} \quad (2)$$

The f_{ar} value for the days in-between two consecutive measurements were obtained by linear interpolation. Absorbed global radiation accumulated from 1st node stage to grain maturity (AR) was calculated by the sum of the daily values of absorbed global radiation, the product of the daily values of f_{ar} and global radiation.

Radiation use efficiency (RUE) was calculated as the slope of the regression of AR on above-ground biomass. Harvest index was calculated by dividing grain yield by aboveground biomass at grain maturity.

Table 2
Monthly means of temperature, global radiation, precipitation and irrigation over the main growing season in 2014, 2015 and the period between 1980 and 2010.

	Temperature (°C)			Global radiation (W m^{-2})			Precipitation (mm)			Irrigation[1] (mm)	
	2014	2015	1980–2010	2014	2015	1980–2010	2014	2015	1980–2010	2014	2015
March	7.6	5.9	4.3	118	99	97	7	42	51	0	0
April	11.5	8.8	8.9	162	192	162	41	43	43	11	8
May	12.9	12.5	13.4	195	213	210	94	15	52	19	43
June	16.0	15.7	16.0	230	223	223	60	37	68	38	73
July	20.3	19.2	18.2	236	220	213	27	104	63	18	38

[1] Water use differed considerably among plants grown under the different CO_2 and N levels. Therefore, irrigation was adapted to the differing water demands and only the irrigation means over the two CO_2 and three N levels are presented.

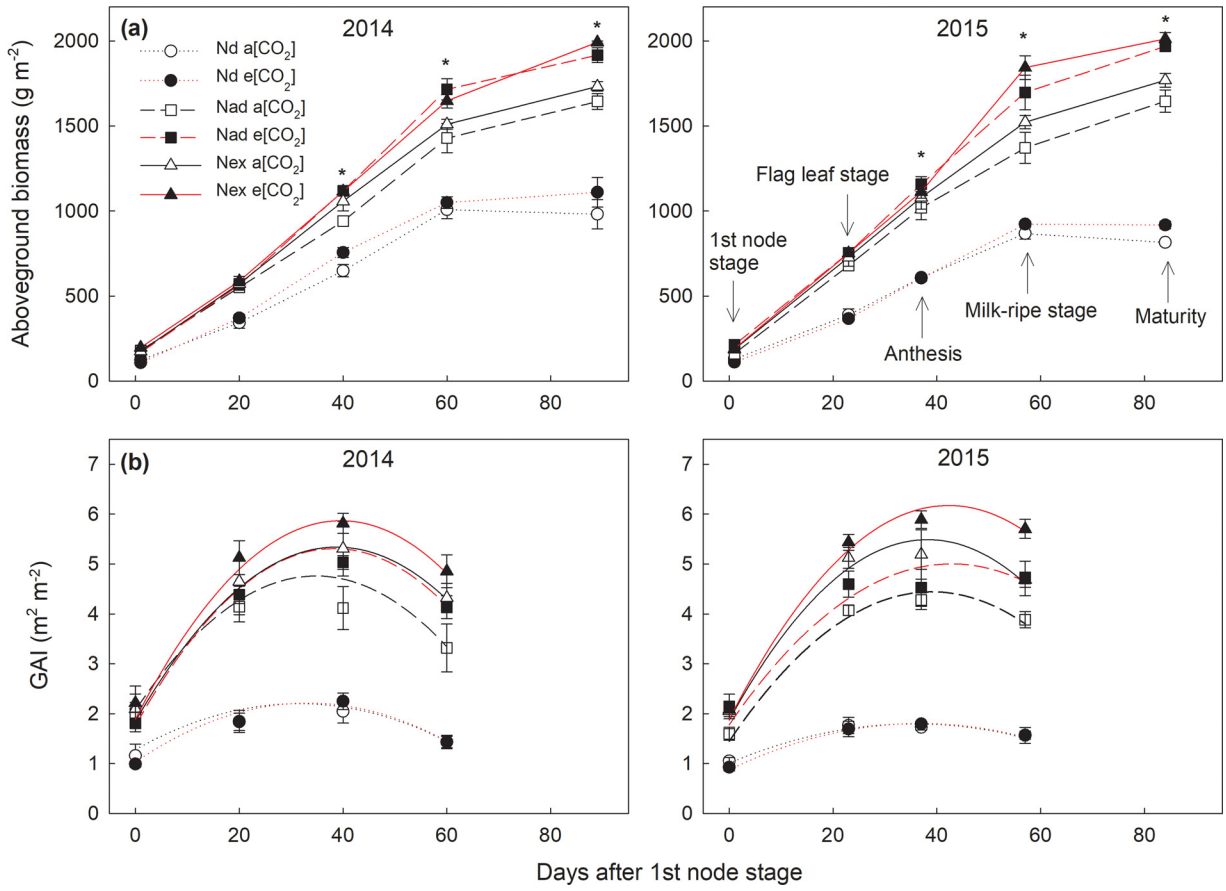

Fig. 1. Time course of aboveground biomass (AGBM) (a) and green area index (GAI) (b) of the two CO_2 and three N levels in 2014 and 2015. Time course of AGBM and GAI is shown from 1st node-stage up to maturity and milk-ripe stage, respectively. Presented are mean values ± standard error (n = 3). Table S1 shows the statistical analysis of the time courses and the asterisks point to the samplings at which significant differences between the marginal CO_2 means (CO_2 means across over all N treatments) ($^*P < 0.05$) were observed. Nd = severe N deficiency; Nad = adequate; and Nex = excess N level. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article).

2.6. Determination of specific leaf weight, green leaf N concentration and specific leaf N weight

Specific leaf weight (SLW) was determined as the quotient from biomass and area of the green leaf blade fraction of the harvest subsamples described in Section 2.4. N concentration was determined via grinding dried leaf blades to a fine powder in a rotor mill (Brabender, Germany) followed by N concentration determination using an element analyzer (Leco TruSpec CNS, USA). Specific leaf N weight (SLNW) was determined by multiplying SLW with leaf blade N concentration.

2.7. Statistics

The experiment was analyzed as split plot design with the CO_2 treatment as main plot factor and the N treatment as sub plot factor and the year effect with repeated measurements because the CO_2 and N treatments had the same position on the field in both years. F-tests were carried out with SAS (version 9.4) proc mixed with the following mixed model:

$$y = \mu + CO_2 + N + Y + CO_2 x N + CO_2 x Y + N x Y + CO_2 x N x Y + R + R x N \quad (3)$$

where y is the dependent variable; μ the overall mean; CO_2 the CO_2 effect; N the N fertilizer effect; Y the year effect; CO_2 x N, CO_2 x Y, N x Y and CO_2 x N x Y the interaction effects; R the main plot error and R x N the residual error. To model the variance/covariance between both years of the main plot and residual error, the UN(1) model was used. This model applies no covariance but allows different error variances for each year.

For the investigation of the CO_2 and N effect on aboveground biomass, GAI, SLW, green leaf N concentration and SLNW over the main growing season in each year the year effect of Eq. (3) was replaced by the effect of sampling. To model the variance/covariance of the main plot and residual error, the best model with regard to the lowest Akaike Information Criterion (AIC) value was selected from six candidate models. Table S1 contains a brief description of the used models.

Least square difference (LSD) tests were carried out with SAS (version 9.4) proc glimmix and means were regarded as different if $P < 0.05$.

Analysis of covariance of the effect of CO_2 and leaf area index (LAI) on SLNW was implemented by sequential F-tests with SAS proc mixed and F-tests were adjusted for the effect of LAI and CO_2 to test the CO_2 and LAI effect, respectively.

The relation of SLNW and leaf area index and of grain yield and level of N fertilizer was reported by quadratic regression (SAS proc mixed) with the following mixed model:

$$y = \mu + CO_2 + \gamma_{co_2 1} x + \gamma_{co_2 2} x^2 + Y + R + R x N + Y x R + Y x R x N \quad (4)$$

where y is the dependent variable; μ the overall intercept; CO_2 the parameter for the two CO_2 treatments altering the intercept; γ_{CO2} the parameters for the linear and quadratic term of the two CO_2 treatments; x the quantitative covariable; Y the random year effect, R the random main plot error; R x N the random subplot error; Y x R the random year

effect main plot error interaction; and Y x R x N the residual error.

3. Results

3.1. Growing conditions

Monthly mean temperature and global radiation were in the range of normal variation in both years and did hardly differ from the long-term average (Table 2). Nevertheless, monthly average temperature in April 2014 (11.5 °C) was somewhat higher compared to 2015 (8.8 °C) and the long-term average (8.9 °C). The amount of precipitation in May and June was considerably lower in 2015 compared to 2014 and the long-term average, respectively, but this water deficit was compensated by manual irrigation.

3.2. Vegetative growth of winter wheat

Fig. 1 shows the evolution of aboveground biomass (AGBM) and green area index (GAI) over the growing season. Both variables were strongly influenced by the level of N fertilizer, because for AGBM and GAI there were considerable differences between plants grown under severe N deficiency (Nd), adequate (Nad) and excess N supply (Nex). AGBM was significantly increased by e[CO_2] from anthesis onwards in both years, except for Nd in 2015 where a significant increase was only detected at maturity. GAI was increased under e[CO_2] primarily from flag leaf emergence onwards in both years, but this was only significant under Nad and Nex in 2015. Thus, in 2015 the CO_2 x N interaction was significant for AGBM and GAI. Across all N levels, peak GAI values were in the range of 2.0 to 5.8 in 2014 and 1.8 to 5.9 in 2015 and were increased by e[CO_2] by 10 to 22% in 2014 and 4 to 19% in 2015 (Fig. 1).

The increase of AGBM and GAI by e[CO_2] was associated with enhanced stem, ear and leaf growth (Table 3). At anthesis in both years, e[CO_2] significantly increased the variables AGBM, stem biomass, GAI, leaf area index, stem area index and stand height in all N treatments. Ear biomass was significantly increased by e[CO_2] only in plants grown under Nad and ear area index was significantly increased by e[CO_2] in plants grown under Nad and Nex but not under Nd. Averaged over both years, e[CO_2] increased stem biomass by 9, 17 and 5%, ear biomass by 4, 17 and 8%, and leaf biomass by 6, 7 and 5% in plants grown under Nd, Nad and Nex, respectively.

3.3. Wheat growth and yield variables at grain maturity

Table 4 presents the mean values of variables determining growth and yield of winter wheat at maturity. All variables were significantly influenced by the N level as well as experimental year as demonstrated by a significant year effect or N x year interaction (Table S2). AGBM as well as stem and leaf biomass were significantly increased by e[CO_2] in all N treatments in both years. Averaged over both years, AGBM was increased by 13, 18 and 14%, stem biomass by 18, 21 and 14% and leaf biomass by 8%, 17% and 4% in plants grown under Nd, Nad and Nex, respectively.

With respect to yield variables, significant CO_2 x N interactions were detected for ear biomass, grain yield and grain number per m^2 ground area (Table 4). These interactions were because e[CO_2] increased these variables significantly under Nad and Nex, but not under Nd. Averaged over both years, grain yield was greater by 10, 17 and 17%, grain number per m^2 ground area by 8, 12 and 12%, and ear biomass by 10, 17 and 16% in plants grown under the Nd, Nad and Nex level, respectively (Table 4). The rise of grain number per m^2 was due to increased ear number per m^2 ground area, whereas e[CO_2] did not influence grain number per ear. 1000 grain weight was not significantly influenced by e[CO_2].

3.4. Radiation absorption, radiation use efficiency and harvest index

Absorbed radiation accumulated over the main growing season (AR), radiation use efficiency (RUE) and harvest index were significantly influenced by the level of N supply (Table 5). AR increased with rising N supply. RUE was similar under Nad and Nex but significantly higher compared to Nd. Harvest index was highest under Nad, but decreased with increasing and decreasing N level.

e[CO_2] did not significantly influence AR, although e[CO_2] increased AR slightly by 4% in 2014 and 10% in 2015 (Table 5). RUE was significantly increased by e[CO_2] in plants grown under Nad (22% in 2014 and 18% in 2015) and Nex (15% in 2014 and 20% in 2015) but not under Nd. Harvest index was slightly but significantly ($P < 0.01$) decreased by e[CO_2] in plants grown under Nd (-1 in 2014 and -5% in 2015).

3.5. Specific leaf weight, green leaf N concentration and specific leaf N weight

Fig. S1 shows the time course of specific leaf weight (SLW), green leaf N concentration and specific leaf N weight (SLNW) and Table S1 the corresponding statistical analysis. SLW was significantly higher in plants grown under Nd compared to the other N levels, however, SLW was not influenced by e[CO_2]. Green leaf N concentration and SLNW declined strongly with progressing growth stage and decreasing N supply. However, green leaf N concentration and SLNW were only slightly decreased by e[CO_2]. Averaged over all samplings, e[CO_2] decreased green leaf N concentration by −8, −3 and −4% in 2014 and −6, −9 and −3% in 2015 under Nd, Nad and Nex, respectively. SLNW was decreased by −6% under each N treatment in 2014, and by −7, −11, −4% under Nd, Nad and Nex, respectively, in 2015. The reduction of green leaf N concentration and SLNW by e[CO_2] were only significant in 2015.

3.6. Relation between leaf area index and specific leaf N weight

Fig. 2 shows the linear regression between leaf area index (LAI) and SLNW based on data of the harvests taken at 1st node stage, flag leaf stage and anthesis while Table S3 shows the results of analysis of covariance of the CO_2 and LAI effect on SLNW within each year x N combination. The variation of LAI explained a large part of the variation of SLNW ($0.29 \leq r^2 \leq 0.71$) and SLNW declined significantly with increasing LAI in all six CO_2 x N combinations in both years. This decline occurred under relative low SLNW values (1.04 to 2.25 g N m^{-2}) under Nd and under higher SLNW values under Nad and Nex ranging from 1.43 to 3.10 g N m^{-2} (Nad) and from 1.66 to 3.33 g N m^{-2} (Nex). With respect to the CO_2 effect, no significant CO_2 x LAI interaction was detected by means of analysis of covariance, indicating the same slope of the regression lines of ambient [CO_2] and e[CO_2]. SLNW was significantly reduced by e[CO_2] regardless of LAI under Nd in 2015 but not in all other year x N combinations.

3.7. Relation between specific leaf N weight and radiation use efficiency

In both CO_2 treatments, RUE increased with rising SLNW in a quadratic manner (Fig. 3). The slope of the RUE x SLNW regression was highest at low SLNW values and declined under increasing SLNW. The initial increase of RUE with rising SLNW values was markedly higher under e[CO_2] compared to ambient [CO_2] which also means much stronger reduction of RUE with decreasing SLNW under e[CO_2].

4. Discussion

The objective of the present FACE study was to detect interactions between e[CO_2] and widely differing levels of N fertilization on wheat growth and yield as well as on important growth parameters, which are

Table 3
Effect of the two CO_2 and three N levels on wheat growth at anthesis. Shown are mean values (n = 3) and the percentage effect of e[CO_2] (Δ (%)). Different small letters indicate significant differences among the marginal means of the N treatments. Asterisks next to the e[CO_2] symbol indicate that the F-test (Table S2) resulted in a significant CO_2 effect, but no significant CO_2 x N and CO_2 x year interaction. If the F-test resulted in a significant CO_2 x N interaction, then different capital letters indicate significant differences for CO_2 means separate for each N treatment and different small letters show significant differences for N means separate for each CO_2 treatment (letters are in bold for e[CO_2]). All letters refer to the means over both years.

	2014			2015		
	Nd	Nad	Nex	Nd	Nad	Nex
AGBM (g m^{-2})						
a[CO_2]	649 c	941 a	1058 a	609 b	1019 a	1080 a
e[CO_2]*	756 c	1118 a	1116 a	606 b	1158 a	1113 a
Δ (%)	17	19	5	−1	14	3
Stem BM (g m^{-2})						
a[CO_2]	452 c	600 a	644 a	407 b	663 a	670 a
e[CO_2]*	528 c	721 a	690 a	413 b	767 a	693 a
Δ (%)	17	20	7	2	16	3
Leaf BM (g m^{-2})						
a[CO_2]	100 c	188 b	238 a	96 c	187 b	224 a
e[CO_2]	116 c	210 b	237 a	94 c	196 b	240 a
Δ (%)	16	12	0	−3	5	7
Ear BM (g m^{-2})						
a[CO_2]	97 A c	154 B b	176 A a	106 A c	169 B b	186 A a
e[CO_2]	113 A **b**	186 A **a**	189 A **a**	99 A **b**	195 A **a**	203 A **a**
Δ (%)	16	21	7	−7	15	9
GAI (m^2 m^{-2})						
a[CO_2]	2.04 c	4.12 b	5.31 a	1.73 c	4.28 b	5.19 a
e[CO_2]*	2.25 c	5.03 b	5.82 a	1.79 c	4.52 b	5.89 a
Δ (%)	10	22	10	4.	6	13
LAI (m^2 m^{-2})						
a[CO_2]	1.21 c	2.61 b	3.46 a	1.03 c	2.90 b	3.49 a
e[CO_2]	1.38 c	3.35 b	3.95 a	1.10 c	2.96 b	3.93 a
Δ (%)	15	28	14	6	2	12
SAI (m^2 m^{-2})						
a[CO_2]	0.65 c	1.17 b	1.46 a	0.52 c	1.08 b	1.35 a
e[CO_2]*	0.66 c	1.30 b	1.45 a	0.54 c	1.23 b	1.55 a
Δ (%)	1	11	−1	3	14	15
EAI (m^2 m^{-2})						
a[CO_2]	0.185 A c	0.328 B b	0.398 B a	0.172 A c	0.294 B b	0.352 B a
e[CO_2]	0.203 A **c**	0.382 A **b**	0.422 A **a**	0.162 A **c**	0.337 A **b**	0.389 A **a**
Δ (%)	10	16	6	−6	15	11
Stand height (m)						
a[CO_2]	0.812 c	0.950 b	0.980 a	0.706 c	0.866 b	0.908 a
e[CO_2]*	0.863 c	0.983 b	1.02 a	0.760 c	0.934 b	0.959 a
Δ (%)	6	4	4	8	8	6

also used in crop growth models (i.e. absorbed radiation by the green canopy accumulated over the growing season (AR), radiation use efficiency (RUE) and harvest index). Also, the CO_2 x N interaction on green leaf N concentration, which influences photosynthesis and RUE (Sinclair and Horie, 1989) and is altered by N supply and e[CO_2] (Kimball et al., 2002), was analyzed.

4.1. Biomass production and grain yield

Starting from anthesis aboveground biomass (AGBM) was increased by e[CO_2]. From the 1st node stage up to flag leaf emergence, average air temperature was low (below 12 °C) but then it exceeded 15 °C. This coincidence of growth stimulation by e[CO_2] with higher temperature is consistent with other experimental data (Shimono et al., 2008) and the theoretical prediction that e[CO_2] increases photosynthesis only when temperatures exceed 10 °C (Long, 1991).

The increase of AGBM by e[CO_2] at grain maturity (13, 18 and 14% under Nd, Nad and Nex) is in agreement with other FACE studies. For example, if the e[CO_2] effect is recalculated for the [CO_2] increase of 210 ppm, then AGBM in spring wheat was increased under adequate N supply by 17% (Högy et al., 2009) as well as by 16–19% in winter wheat (Kou et al., 2007; Weigel and Manderscheid, 2012). For winter wheat grown under moderate N deficiency, an increase of 9 and 14% was found in FACE studies in China (Kou et al., 2007) and on the same field site of the present study (Weigel and Manderscheid, 2012). Increases of 6% (severe N deficiency) and 9% (ample N supply) were reported by Kimball et al. (2002) for spring wheat in Arizona and an increase of 28% was reported for winter wheat grown under ample N supply in China (Ma et al., 2007).

The growth data at anthesis and grain maturity show that while stem and ear growth were similarly enhanced by e[CO_2] this effect was larger than the stimulation of leaf growth. These results are in agreement with other FACE studies (Liu et al., 2008; Manderscheid et al., 2009) and are probably due to the different temperature conditions at these growth stages and the resulting CO_2 x temperature interaction on photosynthesis (Long, 1991).

In the present study, grain yield under ambient [CO_2] and adequate N supply corresponded to empirical data for the local wheat growing area and was higher compared to other FACE studies (Fig. 4), whereas the relative and absolute yield reduction by N deficiency was much stronger than in other studies. The significant N x year interaction on grain number might be partly explained by different climatic conditions. The photothermal quotient 30 days before anthesis that is important to determine grain number (Fischer, 1985) was about 10%

Table 4
Effect of the two CO_2 and three N levels on growth and yield variables at maturity. Shown are mean values (n = 3) and the percentage effect of e[CO_2] (Δ (%)). Different small letters indicate significant differences among the marginal means of the N levels. Asterisks next to the e[CO_2] symbol indicate that the F-test (Table S2) resulted in a significant CO_2 effect, but no significant CO_2 x N and CO_2 x year interaction. If the F-test resulted in a significant CO_2 x N interaction, then different capital letters indicate significant differences for CO_2 means separate for each N treatment and different small letters show significant differences for N means separate for each CO_2 treatment (letters are in bold for e[CO_2]). All letters refer to the means over both years.

	2014			2015		
	Nd	Nad	Nex	Nd	Nad	Nex
AGBM (g m^{-2})						
a[CO_2]	981 B c	1644 B b	1732 B a	816 B c	1646 B b	1769 B a
e[CO_2]	1110 A **b**	1917 A **a**	1993 A **a**	918 A **b**	1968 A **a**	2012 A **a**
Δ (%)	13	17	15	13	20	14
Stem BM (g m^{-2})						
a[CO_2]	340 B c	553 B b	598 B a	265 B c	541 B b	616 B a
e[CO_2]	400 A **b**	657 A **a**	680 A **a**	316 A **b**	666 A **a**	704 A **a**
Δ (%)	18	19	14	19	23	14
Leaf BM (g m^{-2})						
a[CO_2]	68 c	112 b	142 a	46 c	97 b	123 a
e[CO_2]*	68 c	125 b	144 a	54 c	118 b	132 a
Δ (%)	1	12	2	18	22	8
Ear BM (g m^{-2})						
a[CO_2]	574 A b	979 B a	993 B a	505 A b	1008 B a	1030 B a
e[CO_2]	642 A **b**	1134 A **a**	1169 A **a**	548 A **b**	1185 A **a**	1175 A **a**
Δ (%)	12	16	18	9	18	14
Grain yield (g m^{-2})						
a[CO_2]	472 A b	817 B a	818 B a	417 A b	831 B a	829 B a
e[CO_2]	528 A **b**	949 A **a**	971 A **a**	446 A **b**	973 A **a**	948 A **a**
Δ (%)	12	16	19	7	17	14
Grain number (m^{-2})						
a[CO_2]	10248 A c	17827 B b	18977 B a	9342 A c	19236 B b	21873 B a
e[CO_2]	11488 A **c**	20032 A **b**	21416 A **a**	9691 A **c**	21607 A **b**	24254 A **a**
Δ (%)	12	12	13	4	12	11
Ear number (m^{-2})						
a[CO_2]	314 c	430 b	451 a	292 c	420 b	529 a
e[CO_2]*	323 c	461 b	502 a	313 c	476 b	559 a
Δ (%)	3	7	11	7	13	6
Grain number (ear^{-1})						
a[CO_2]	32.8 b	41.5 a	42.8 a	32.0 b	45.8 a	41.4 a
e[CO_2]	35.4 b	43.5 a	42.7 a	31.0 b	45.4 a	43.5 a
Δ (%)	8	5	0	−3	−1	5
TGW (g)						
a[CO_2]	46.1 a	45.9 a	43.1 b	44.7 a	43.2 a	37.9 b
e[CO_2]	45.9 a	47.4 a	45.4 b	46.1 a	45.0 a	39.1 b
Δ (%)	0	3	5	3	4	3

Table 5
Effect of the two CO_2 treatments and three N levels on radiation absorption accumulated from 1st node stage up to maturity (AR), radiation use efficiency (RUE) and harvest index. Presented are mean values (n = 3) and the percentage effect of e[CO_2] (Δ (%)). Different small letters indicate significant differences among the marginal means of the N levels. If the F-test (Table S2) resulted in a significant CO_2 x N interaction, then different capital letters indicate significant differences for CO_2 means separate for each N treatment and different small letters show significant differences for N means separate for each CO_2 treatment (letters are in bold for e [CO_2]). All letters refer to the means over both years.

	2014			2015		
	Nd	Nad	Nex	Nd	Nad	Nex
AR (MJ m^{-2})						
a[CO_2]	826 c	1205 b	1293 a	682 c	1141 b	1293 a
e[CO_2]	863 c	1216 b	1295 a	748 c	1160 b	1296 a
Δ (%)	4	1	0	10	2	0
RUE (g MJ^{-1})						
a[CO_2]	1.09 A b	1.21 B a	1.21 B a	1.08 A b	1.29 B a	1.24 B a
e[CO_2]	1.17 A **b**	1.47 A **a**	1.39 A **a**	1.12 A **b**	1.52 A **a**	1.48 A **a**
Δ (%)	8	22	15	4	18	20
Harvest index						
a[CO_2]	0.481 A a	0.497 A a	0.472 A b	0.511 A a	0.505 A a	0.469 A b
e[CO_2]	0.475 B **b**	0.495 A **a**	0.487 A **b**	0.487 B **b**	0.494 A **a**	0.471 A **b**
Δ (%)	−1	0	3	−5	−2	1

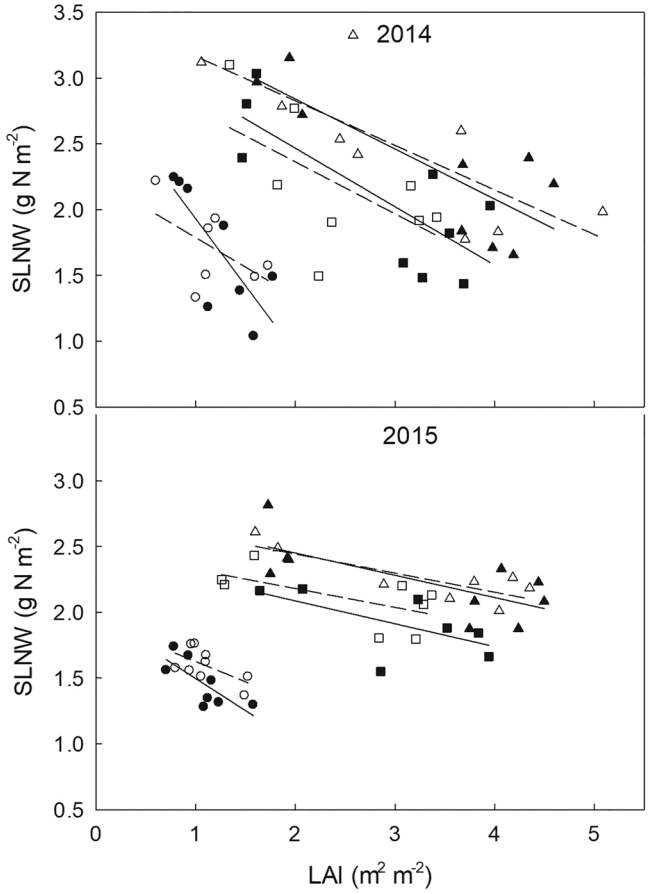

Fig. 2. Linear regression of leaf area index (LAI) on specific leaf N weight (SLNW) among the values of the harvests taken at 1st node stage, flag leaf stage and anthesis in 2014 (top) : Nd and a[CO_2] (○) $r^2 = 0.29$, $P = 0.21$; Nd and e[CO_2] (●) $r^2 = 0.61$, $P < 0.05$; Nad and a[CO_2] (□) $r^2 = 0.33$, $P = 0.14$; Nad and e[CO_2] (■) $r^2 = 0.61$, $P < 0.01$; Nex and a[CO_2] (Δ) $r^2 = 0.58$, $P < 0.05$; Nex and e[CO_2] (▲) $r^2 = 0.58$, $P < 0.01$; and in 2015 (bottom): Nd and a[CO_2] (○) $r^2 = 0.36$, $P < 0.10$; Nd and e[CO_2] (●) $r^2 = 0.56$, $P < 0.05$; Nad and a[CO_2] (□) $r^2 = 0.38$, $P = 0.11$; Nad and e[CO_2] (■) $r^2 = 0.38$, $P = 0.14$; Nex and a[CO_2] (Δ) $r^2 = 0.71$, $P < 0.01$; Nex and e[CO_2] (▲) $r^2 = 0.48$, $P < 0.05$.

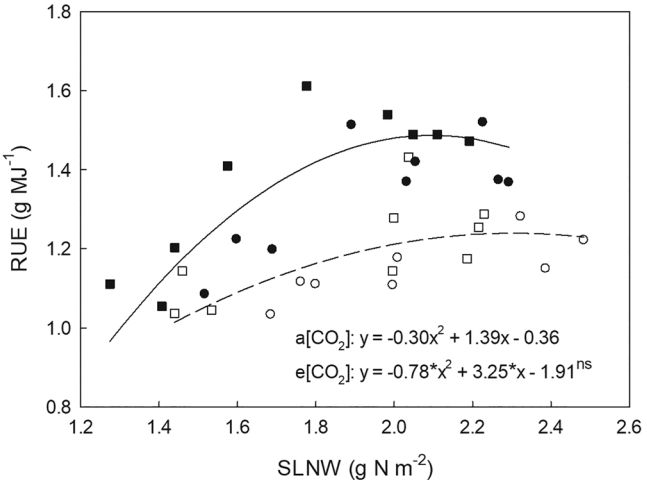

Fig. 3. Regression of radiation use efficiency (RUE) on specific N weight of green leaves (SLNW). To implement this regression the means of SLNW over the three and four harvests in 2014 and 2015, respectively were used. The circles and squares indicate the data of 2014 and 2015, respectively. Open symbols and dashed line = ambient [CO_2] and closed symbols and solid line = e[CO_2]. The equations describe the regression curves, where y = RUE and x = SLNW. Asterisks indicate significant differences ($P < 0.05$) between the parameters of the ambient [CO_2] and e[CO_2] treatment.

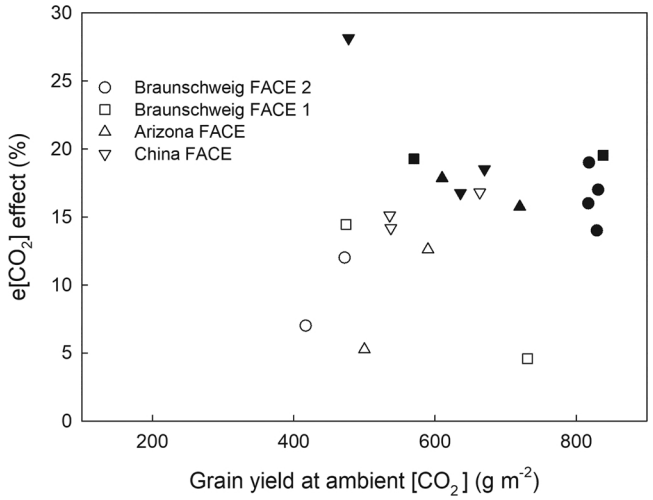

Fig. 4. Overview of the effect of e[CO_2] on grain yield of different FACE studies with several N fertilization levels and sufficient water supply. The percentage effect of e[CO_2] was normalized to the [CO_2] increase of 210 ppm. White symbols = N deficiency and black symbols = ample N supply. The data sources are the following: Braunschweig FACE 2 = data of the present study; Braunschweig FACE 1 = Weigel and Manderscheid (2012); Arizona FACE = Jamieson et al. (2000) and Kimball et al. (2002); China FACE = Kou et al. (2007)*, Ma et al. (2007)* and Han et al. (2015). *Grain yield was calculated from biomass, assuming a harvest index of 0.5.

larger in 2015 compared to 2014 (data not shown) and thus was possibly responsible for the larger grain number under adequate (8%) and excess N supply (14%) in 2015. The grain yield stimulation by e[CO_2] in the present study (10, 17 and 17% under Nd, Nad and Nex) is in agreement with other FACE studies (Kimball et al., 2002; Weigel and Manderscheid, 2012; Han et al., 2015). However, higher yield stimulation up to 35% and 47% were found at FACE sites in semi-arid regions in Australia (Tausz-Posch et al., 2012, 2015) and China (Lam et al., 2012), respectively where N availability was unlimiting.

The regression of N fertilizer level on grain yield (Fig. 5) suggests that the yield stimulation by e[CO_2] in the present study increased with N supply up to a certain N amount. This is in line with the two-year Arizona FACE study, where e[CO_2] hardly increased grain yield (5%) under severe deficiency (15 kg N ha^{-1}) in the 2nd year, but the yield increase by e[CO_2] was considerably stronger (12%) under less severe N deficiency (70 kg N ha^{-1}) in the 1st year (Kimball et al., 2002).

4.2. Radiation absorption and radiation use efficiency

Green area index (GAI) and AR were markedly influenced by the N level as was observed in many other studies (e.g. Garcia et al., 1988; Sieling et al., 2016). Previous FACE experiments with wheat reported various effects of e[CO_2] on the size of GAI: a decrease under N deficiency (Brooks et al., 2000; Jamieson et al., 2000), an increase and decrease under adequate N supply (Bunce, 2016; Cai et al., 2016), and an increase under excess N supply (Brooks et al., 2000; Jamieson et al., 2000). In the present study, GAI was increased by e[CO_2] under all N levels, while AR was not influenced, but tended to be increased by e[CO_2] under N deficiency. For the adequate and excess N level, the increases in GAI under e[CO_2] became apparent only after flag leaf emergence when the soil was already completely covered by the canopy so that the rise of GAI hardly altered AR but increased light attenuation within the canopy. However, under severe N deficiency where GAI was very low (≤2.2) the slight increase of GAI under e[CO_2] resulted in a slight increase of AR. These results are in contrast with those obtained in the Arizona FACE experiment where GAI was much higher (≤3.8)

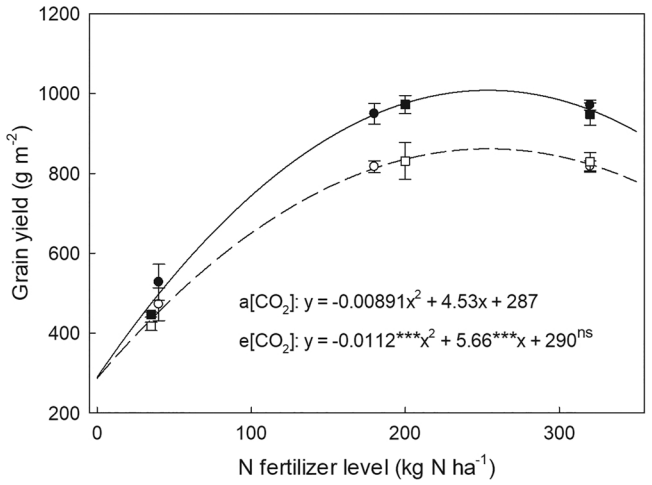

Fig. 5. Regression of grain yield on total amount of N fertilizer. Presented are the mean values (n = 3; ± S.E.M) and corresponding regression curves for the ambient [CO_2] (dashed line) and e[CO_2] treatment (solid line). Circles and squares indicate the data of 2014 and 2015, respectively. Open symbols = ambient [CO_2] and closed symbols = e[CO_2]. The integrated equations describe the regression curves, whereby y = grain yield and x = level of N fertilizer. Asterisks indicate significant differences ($P < 0.001$) between the parameters of the ambient [CO_2] and e[CO_2] treatment.

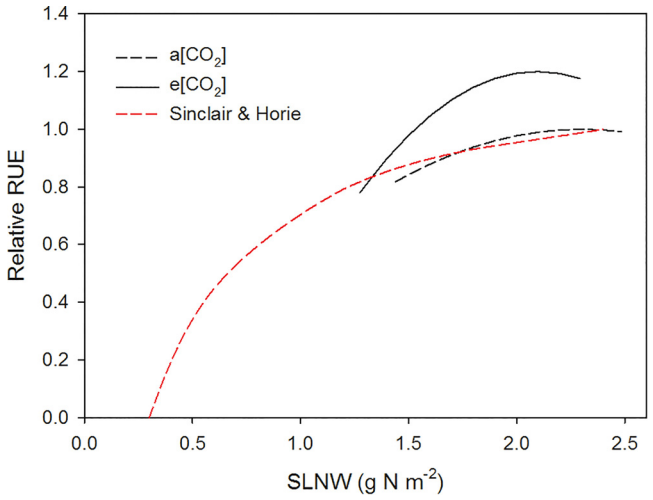

Fig. 6. Relation between relative radiation use efficiency (RUE) and specific N weight of green leaves (SLNW). The ambient [CO_2] (a[CO_2]) and e[CO_2] curves were derived from the regression of RUE on SLNW (Fig. 3). Additionally, the rice data of the relation between RUE and SLNW of Sinclair and Horie (1989) were included. Relative RUE was derived by normalization with the maximum RUE at ambient [CO_2] and of Sinclair and Horie (1989), respectively.

under comparable severe N deficiency (70 and 15 kg N ha^{-1}) and e[CO_2] reduced both the size and duration of GAI and thus AR, leading to the reduction of grain yield stimulation by e[CO_2] (Jamieson et al., 2000).

Photosynthetic capacity and RUE are closely associated variables that are stable over a broad range of leaf and soil N levels, but decline sharply when these become very low (Sinclair and Horie, 1989). In the present study, RUE did not differ between plants grown under adequate and excess N supply but declined under severe N deficiency, which is in agreement with other studies (e.g. Garcia et al., 1988; Sieling et al., 2016) and suggests that photosynthetic capacity was also reduced under N deficiency. RUE was strongly increased by e[CO_2] by 20% under adequate and 18% under excess N supply, which is consistent with the value (17%) used in the SIRIUS growth model (Jamieson et al., 2000), but hardly under severe N deficiency (6%).

Fig. 6 compares the relationship between RUE and SLNW of the present study and the one of Sinclair and Horie (1989). At ambient [CO_2], there was a good correspondence of relative RUE in the overlaying SLNW area where RUE was hardly affected by decreasing SLNW. However, at e[CO_2] RUE declined significantly stronger with decreasing SLNW compared to ambient [CO_2]. Thus, crop models using RUE to calculate biomass production should include the different dependence of RUE on SLNW under ambient [CO_2] and e[CO_2].

The CO_2 x N interaction on RUE of the present study indicates that the smaller yield stimulation by e[CO_2] under N deficiency compared to high N was associated with a smaller effect of e[CO_2] on RUE, but not on AR as was observed in the Arizona FACE experiment (Jamieson et al., 2000).

4.3. Green leaf N concentration

In the Arizona FACE study a strong decline in leaf N concentration by e[CO_2] was detected under severe N deficiency (Sinclair et al., 2000) which was on average −25% in the 1st and −19% in the 2nd year, but leaf N concentration was not affected under ample N supply (Kimball et al., 2002). Based on those and other results of several enclosure studies (Stitt and Krapp, 1999), it was concluded that downregulation of photosynthetic capacity by e[CO_2] in wheat primarily occurs under N deficiency (Wall et al., 2000; Rubio-Asensio and Bloom, 2016). However, in contrast to Sinclair et al. (2000), but in agreement with Tausz et al. (2017), in the present study the reduction of leaf N concentration was very similar among N levels with values of −7, −6, −4% under severe N deficiency, adequate and excess N supply, respectively. Because specific leaf weight (SLW) was not influenced by e[CO_2] in the present study, the reduction of SLNW corresponded to the reduction of leaf N concentration.

SLNW decreases within the canopy from the top to the bottom because of light attenuation (Hirose, 2005; Bertheloot et al., 2008). In the present study, the effect of e[CO_2] on LAI corresponded to the one on GAI with an increase from flag leaf emergence under all N levels in 2014 and a general increase under adequate and excess N supply in 2015 (data not shown). In the present study, SLNW decreased with increasing LAI and this relation was not influenced by e[CO_2] under adequate and excess N supply, but only under severe N deficiency. These results suggest that the decline in SLNW under e[CO_2] and high N supply was primarily due to the increase of GAI and resulting adaption of the leaves down in the canopy to higher light attenuation under e[CO_2]. Nie et al. (1995) reported similar results based on a FACE study with ample N supply where leaf RuBisCO content was not declined by e[CO_2] until LAI was increased by e[CO_2] (Kimball et al., 1995). Also, another FACE study showed no influence of e[CO_2] on the relation between LAI and leaf N content per m^2 ground area under ample N supply (Cai et al., 2016). The herein observed reduction of SLNW under e[CO_2] regardless of the effect of LAI under severe N deficiency suggests that a direct e[CO_2] induced reduction of leaf N concentration occurs in field grown wheat primarily only under very low soil N availability.

4.4. Mechanism of the lower RUE associated yield stimulation of e[CO_2] under severe N deficiency

As shown above, the stimulation of RUE as well as ear growth and related variables (grain number and grain yield) of e[CO_2] were lower under severe N deficiency compared to high N supply. These CO_2 x N interactions might be partly explained by the fact that the small reduction of SLNW by e[CO_2] under severe N deficiency brought about a reduction in photosynthetic capacity. However, there is indication that insufficient N supply for ear growth was also involved. The regression of SLNW on RUE (Fig. 3) shows that RUE was elevated under e[CO_2] but declined stronger with decreasing SLNW under e[CO_2] compared to ambient [CO_2], which is indicative of increasing N shortage with

respect to plant growth under rising N deficiency. Given that RuBisCO content would only limit RUE stimulation under e[CO_2] one would rather expect parallel curves for both CO_2 treatments. Moreover, in the present study, harvest index was reduced by e[CO_2] under severe N deficiency because of the strong stimulation of stem growth by e[CO_2] and the CO_2 x N interaction on ear growth and related variables. According to van Kraalingen (1990), additional assimilates from growth under e[CO_2] are primarily allocated to organs with low N contents when soil N supply is deficient. Because ear N concentration is about twice as much than the one of stem, this concept might explain the decrease of harvest index. This decrease of harvest index indicates that under e[CO_2] severe N deficiency induced an imbalance between photosynthetic capacity (source) and ear growth (sink capacity), where the latter seems to be more restrictive with respect to the grain yield stimulation by e[CO_2]. The competiton for N between stems and ears could be mitigated by changing the temporal pattern of N fertilization by adding more fertilizer around booting and less before this stage. However, as water availability is critical for the effect of N fertilization but is often strongly limited in developing countries, this strategy could there not be readily feasible.

In conclusion, the present field study shows that only a small grain yield stimulation by e[CO_2] can be expected for wheat grown under severe N deficiency but adequate water supply. Moreover, Walker et al. (2017) showed that grain yield stimulation was not present at all under N deficiency and limited water availability. Hence, CO_2 fertilization might not be an important factor in counteracting negative climate change effects on wheat yields primarily in developing countries where high N fertilizer levels are hardly affordable. This reduced yield reaction to e[CO_2] was not due to a decreased AR caused by accelerated canopy senescence under e[CO_2] as was observed in the Arizona FACE study (Jamieson et al., 2000). Rather, it was due to a decreased RUE stimulation later in the season, which was attributed to a deficiency of N for ear growth and a reduction of photosynthetic capacity by e[CO_2] where the former seemed to have a larger impact. It remains to be investigated whether grain yield stimulation by e[CO_2] under severe N deficiency can be increased by adjusting the timing of N fertilization, i.e. applying more fertilizer at booting and less before.

Conflict of interest

None of the authors has any conflict of interest to declare.

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Appendix A. Supplementary data

Supplementary material related to this article can be found, in the online version, at doi: https://doi.org/10.1016/j.eja.2018.08.007.

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